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The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone

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Abstract

In a mountain context, the forest-shrub ecotone is an area of high biodiversity. Relatively little is known about the habitat requirements of birds in this habitat, yet it is facing potential threats from changes in grazing practices and climate change. Moreover, it is not clear at which scale habitat associations should be assessed in Alpine birds. Further information on key habitat components affecting bird communities of the ecotone are needed in order to inform management strategies to counteract potential habitat loss, and to better inform predictions of how bird communities may be affected by future environmental change. Data on bird occurrence and broadscale (land cover) and finescale (vegetation structure and shrub species composition) habitat variables were collected in an Alpine forest-shrub ecotone in Val Troncea (northwestern Italian Alps) in order to address two objectives: to identify the key habitat variables associated with the occurrence of individual species and with the diversity of the bird community; and, to assess which scale of habitat measurement (broadscale, finescale or both combined) is needed to model bird occurrence. Broadscale variables, or combinations of broad- and finescale variables, tended to have the best performing models. When combined models performed best, shrub species identity was included in many cases. Shrubs also played an important role in explaining variations in species diversity and richness. Vegetation structure was of relatively little importance, either for individual bird species or for species richness and diversity. These findings suggest that management should strive to maintain a mosaic of habitats whilst minimizing forest encroachment, which could be achieved through targeted grazing. Broadscale habitat data and data on shrub species composition should provide a sufficient basis for identifying relevant species-specific habitat parameters in a mountain environment in order to model future scenarios of effects of habitat change on the bird community of the alpine forest-shrub ecotone.

Introduction

Mountain biodiversity is under a range of environmental pressures, including land use change (Laiolo et al. 2004), increased human leisure activities (Rolando et al. 2007; Arlettaz et al. 2007), climate change (Sekercioglu et al. 2008; Dirnböck et al. 2011), and interactions between these factors (e.g. Brambilla et al. 2016). Climate change may be a particular problem given that the rate of warming in mountains is approximately double the global average, a trend that is expected to continue (Böhm et al. 2001). A consequence of climate change is that vegetation zones are likely to shift upwards – for example, the upper forest limit has shifted to higher elevations in many mountain regions in line with rising temperatures (Harsch et al. 2009). The loss of high altitude open habitats as a consequence of such vegetation shifts has been identified as a potential future conservation problem (Sekercioglu et al. 2008; Chamberlain et al. 2013), especially as the proportion of species of conservation concern tends to increase with elevation (Viterbi et al. 2013). However, vegetation shifts in some areas have also been due to abandonment of grazing which maintained the forest limit at a lower altitude than would be possible under only climatic constraints. This effect has had a greater effect than climate change on treeline shifts in the European Alps (Gehrig-Fasel et al. 2007).

The ecotone between the forest and the alpine grassland zone is characterized by a high structural diversity, typically being a mix of open grassland areas, pioneer forest and shrub species. It is therefore often an area of high biodiversity (Dirnböck et al. 2011). Whilst abandonment of grazing and vegetation shifts due to climate change may, at least initially, have the capacity to create new habitats, in particular through the colonization by shrub species (Laiolo et al. 2004), there are also threats to this habitat. First, it seems plausible to expect that structural diversity is a key factor driving the relatively high biodiversity of the ecotone (e.g. MacArthur and MacArthur 1961), and grazing is likely to maintain a habitat mosaic that underpins the structural diversity, hence further abandonment of grazing may be detrimental. Second, many mountainous areas do not reach altitudes that are high enough

to maintain the ecotone habitat given the likely magnitude of vegetation shifts (Dirnböck et al. 2011) – such areas are likely to be mostly forest in the future. Third, it cannot be assumed that all components of the vegetation community will respond simultaneously to climate change (Theurillat and Guisan 2001). For example, there is evidence that vegetation zones respond differentially to warming temperatures in the Alps (Cannone et al. 2008), and that trees and shrubs may respond differentially to reduced snow cover resulting from climate change. Snow has insulating properties that benefit some shrub species from frost damage (Neuner 2014), and lower snow cover or earlier snow melt could potentially lead to a net loss of ecotone habitat.

Within the gradient of alpine habitats from mountain forest to the highest altitude nival zone (Kapos et al. 2000, Körner & Ohsawa 2006), the highest biodiversity is typically found in the forest-shrub ecotone, yet it has been little studied in an avian context. Whilst common species such as Dunnock *Prunella modularis*, Linnet *Carduelis cannabina*, Lesser Whitethroat *Sylvia curruca* and Wren *Troglodytes troglodytes* have been studied in lowland habitats (usually at higher latitudes), the few studies that have assessed habitat associations in these species in mountain habitats have considered only broadscale, usually remote-sensed, habitat data and have not considered more detailed measures of habitat complexity (Chamberlain et al. 2013, 2016). With a few exceptions, notably Black Grouse *Tetrao tetrix* (e.g. Patthey et al. 2012, Braunisch et al. 2016) and Ring Ouzel *Turdus torquatus* (von dem Bussche et al. 2008), there is as yet insufficient information to determine at which scale species-habitat associations should be assessed in order to plan conservation actions for the majority of common Alpine ecotone species in the context of environmental changes. Furthermore, such studies would also allow the improvement in our ability to forecast potential effects of future environmental change for ecotone species. Species distribution models for typical ecotone species such as Dunnock, Wren and Tree Pipit *Anthus trivialis* show generally less good model performance, and greater inconsistency in model outcomes between different scenarios of change, compared with forest and grassland species (Chamberlain et al. 2013, 2016). This may be because these species are more dependent

on finescale habitat characteristics, such as vegetation structure, and hence are not well-described by land cover and topographic variables that typically underpin many species distribution models.

Heterogeneity plays an important role for bird species diversity in a range of different habitats, including farmland (Benton et al. 2003), rain- (Guerta and Cintra 2014) and temperate forests (Freemark and Merriam 1986) and grasslands (Hovick et al. 2014). However, the role of heterogeneity in the forest-shrub ecotone is still not well understood. We would expect that, based on the influence of habitat diversity and structural vegetation diversity, species richness in the ecotone would be positively associated with measures of habitat heterogeneity. A recent study on Black Grouse in the Swiss Alps showed that horizontal and vertical structural heterogeneity was the best predictor for the occurrence of the species (Patthey et al. 2012). We similarly expect that ecotone species will in general be positively associated with habitat complexity. In this study, we consider complexity in terms of the diversity of vegetation structure, the heterogeneity in vegetation height, and also in terms of the habitat mosaic formed by shrubs, grassland and forest. We focus in particular on non-linear relationships between the bird community and shrub cover as a measure of the habitat mosaic, the expectation being that bird diversity and individual species occurrences will peak at intermediate values of shrub cover.

The specific objectives of this study are (i) to assess key habitat attributes that influence bird diversity and individual species occurrence in an Alpine forest-shrub ecotone, and (ii) to determine whether habitat cover and altitude are adequate to model species distributions in the ecotone, or if more detailed information on vertical vegetation structure and shrub species composition is needed.

Methods

Study area and point selection

The study was carried out in Val Troncea Natural Park (44°57'28" N; 6°56'28" E) in the western Italian Alps. At lower altitudes the area is dominated by larch *Larix decidua*. The natural treeline is typically found at around 2200 m asl, but varies depending on local conditions. Typical shrub species are *Juniperus nana* (henceforth Juniper) and *Rhododendron ferrugineum* (henceforth Rhododendron) which rapidly encroached wide areas of grasslands after the decline of agro-pastoral activities. Grasslands were mainly dominated by *Festuca curvula*, *Carex sempervirens*, and *Trifolium alpinum*. Scree and rocky areas occur predominantly at higher altitudes, above approximately 2700 m asl.

Point counts were carried out in the forest-shrub ecotone, which we defined as the transition zone between forest and alpine grasslands. We included both natural ecotones where the treeline is limited by climatic conditions, and areas where open grassland has been maintained at lower altitudes, mostly due to grazing by domestic livestock, but also due to avalanches in some locations. Point count locations coincided with the centroids of a pre-existing grid at a scale of approximately 150 x 150 m (there was some variation, due to access constraints for example; Probo et al. 2014) along the western facing slope of the valley. Points were selected that had a minimum shrub cover of 5 % and a maximum tree cover of 70 % (i.e. thus presenting the forest-shrub ecotone) within 100 m radius according to vegetation surveys (see below). All points were spaced a minimum of 200 m apart.

Bird surveys

Point counts (n = 79) were carried out from mid-May to mid-July over a period of 2 years (46 in 2015 and 33 in 2016) following the methods of Bibby et al. (2000), using a 10 minute count period. At each point count location, all individual birds seen or heard were recorded within a 100 m radius (estimated with the aid of a laser range finder). Point counts commenced 1-1.5 h after sunrise and continued until 1200 h. Surveys did not take place in excessively wet or windy conditions. Each point count location was visited once.

Broadscale and finescale habitat

Habitat data were defined into two categories representing 'broadscale' habitat data (land cover, altitude and other variables estimated at a resolution of the whole point count location) and 'finescale' habitat data (vegetation structure and shrub species composition estimated from plots at a finer scale of resolution within the point count location). Broadscale habitat comprised visual estimation of the percentage cover of canopy (i.e. vegetation above head height), shrubs (woody vegetation below head height), open grassland and bare rock (including scree and unvegetated areas) within a 100 m radius of the point's centre. The number of mature trees (greater than c. 20 cm in diameter at breast height) within a 50 m radius of a point count location was also counted. These estimates have been shown to correlate well with estimates of land cover derived from remote sensing and have been used as the basis of predictive models for several species considered here (Chamberlain et al. 2013, 2016).

Finescale habitat data on vegetation structure and composition were collected at the centre of the point count location and along two 100 m long transects, each divided into 5 plots spaced 20 m apart originating at the point's centre (therefore there were eleven plots sampled per point count location including the central point). The compass bearing of each transect from the centre of the point to its perimeter was selected at random, the only constraint being that there had to be an angle greater than 90° between two transects at the same point. Following Bibby et al. (2000), at each plot, vegetation density was measured at three different heights (0 m; 0.5 m; 1 m) using a chequered board (50 cm x 30 cm), divided into 10 x 10 cm square subdivisions, placed vertically into the vegetation, the bottom of the board coinciding with the appropriate height class. To produce an index of vegetation density, an estimate was made of the number of squares of the board that were obscured by vegetation observed from a distance of 5 m. A square was considered obscured by vegetation when <50 % of it was visible. The diversity of vegetation density over all 11 plots was then calculated with the Shannon index $H' = - \sum p_i \ln p_i$, where p_i is the proportion of squares obscured at the i th plot. Data were also collected on grass and shrub height (if present), and the standard deviation of height calculated across the 11 plots was used as a

measure of vegetation height heterogeneity for each point. The dominant shrub species at each plot within a 1 m radius was recorded, defined into four groups: Rhododendron, Juniper, bilberry (*Vaccinium myrtillus* and *V. gaultherioides*) and other (e.g. Green Alder *Alnus viridis*, Willow *Salix spp*, and also including young trees less than two meters in height, mostly European Larch *Larix decidua*). The frequency of plots in which a given group was present was calculated for each point (i.e. the maximum frequency was 11). All habitat variables used in the analysis are listed in Table 1 (a complete list of variables measured in the field, but not included in the models due to collinearity, are given in Electronic Supplementary Material (ESM) Table S1).

Data analysis

Birds detected within a 100 m radius of a point count location were used to analyse species richness (simply the number of species detected on each point count), species diversity (expressed using the Shannon index) and species distribution (presence/absence of individual species) with regard to habitat composition and structure within the forest-shrub ecotone.

Data were analysed using an information theoretic approach with the MuMIn package in R (R v.3.3.2, R Development Core Team 2016; Bartoń 2013). This entailed first deriving full models at each scale and for each dependent variable (richness, diversity or species presence) using a mixed modelling approach in the R package lme4 (Bates et al. 2015). Model-averaged parameter estimates were derived for all combinations of variables in each full model in order to identify variables that were most closely associated with bird distribution and diversity. P-values derived from the model-averaged parameter estimates and their standard errors were considered to represent significant effects when $P < 0.05$. In addition, the Akaike Information Criterion corrected for small sample size (AICc) was determined for each individual model and was used to assess model performance at different scales (see below).

Prior to modelling, all variables within each set (i.e. broad- or finescale) were scaled and centred. Variance inflation factors (VIFs) were calculated using the 'corvif' function (package 'AED', Zuur et al. 2009) to assess collinearity between continuous explanatory variables. All variables with a VIF > 3 were sequentially removed from the variable set until all VIFs were < 3. Intercorrelations between remaining variables were then checked, and for those with Spearman correlation coefficients > 0.50, one of the pair was subsequently omitted (variables with a large proportion of zeroes were preferentially omitted, otherwise the choice was random). As a final check, variables that had been removed in the procedure to minimise collinearity were substituted for closely correlated variables (in particular between overall shrub cover or frequency, and the frequency of individual shrub species). Cases where the model with the substituted variable had a lower AICc were used in the final full model. As we were particularly interested in how the shrub-grassland habitat mosaic affected the bird community, we included a quadratic effect of variables representing shrub cover (including the frequency of individual shrub species) in all models. For other variables, non-linear effects were included in the models following visual assessment of scatterplots (following Zuur et al. 2009). Year was specified as random effect in every model to account for possible inter-annual effects.

Species richness and species diversity were analysed using generalised linear mixed models in relation to habitat variables, specifying a Poisson and a normal error distribution respectively. The occurrence probability of the commonest species (present on 15 % of points – Chamberlain et al. 2013 found that models performed persistently poorly below this threshold) in relation to habitat was analysed using binomial logistic regression, each species being recorded as either present or absent per point. At each scale, the residuals for all full models were extracted and tested for spatial autocorrelation using Moran's I (Moran 1950). There was no strong evidence of spatial autocorrelation across species or scales (see details ESM Table S6 and S7), therefore this was not considered further.

At the end of the above process, for species richness and diversity and for each individual species, candidate models with model averaged parameter estimates were

derived for each combination of variables based on the full model for broad- and finescale habitat variables separately. The next step was then to derive combined models based on the most important variables from both broadscale and finescale models, defined as those variables which were either significant ($p \leq 0.05$) or which approached significance ($p \leq 0.1$) from the broad- and finescale model sets. In the few cases where no variables had $P < 0.10$, those with a high Akaike weight (> 0.50) in each scale-specific model were used in the combined model. The new data set was again subject to variable set reduction according to VIFs and correlation coefficients, and subsequently combined models were derived, which were again subject to model averaging.

The extent to which broadscale or finescale habitat structure, or a combination of the two, was necessary to model species diversity and distributions was assessed using AICc. At each scale (finescale, broadscale and combined) and for each dependent variable, models were ordered according to the AICc, where lower values indicate better performing models. Change in AICc relative to the top ranked model was calculated as $\Delta AICc$. Models with $\Delta AICc < 2$ were considered equivalent. Models from all three scales were compared in order to assess whether high model performance was associated with either broadscale or finescale habitat variables, or a combination of both. The importance of each variable at each scale was assessed by calculating Akaike weights based on all combinations of models (Burnham and Anderson 2002), which are expressed as the likelihood contribution of each model as a proportion of the summed likelihood contributions of all models. The weight for each variable is the sum of model weights for all models in which a given variable was present (Burnham and Anderson 2002).

Results

In total, 263 individuals of 29 species were recorded in 79 point counts over an altitudinal range of 1800-2600 m asl. There were eight species that were recorded on at least 15 % of the points: Tree Pipit, Water Pipit *Anthus spinoletta*, Dunnock, Northern Wheatear *Oenanthe*

oenanthe, Lesser Whitethroat, Wren, Chaffinch *Fringilla coelebs*, Rock Bunting *Emberiza*
cia. No significant model averaged parameter estimates could be identified to predict Rock
Bunting occurrence for broad- or finescale models, therefore this species was not
considered in further analyses.

Broadscale habitat structure

Details of model-averaged parameters of the model set for broadscale habitat structure are
given in ESM Table S2. Bird species richness and diversity showed a positive relationship
with the number of mature trees. Shrub cover showed a quadratic effect on bird diversity
whereby diversity increased initially with the percentage of shrub cover, but declined after a
shrub cover of approximately 55 % was reached. Furthermore, diversity was negatively
associated with altitude. Among individual species, Dunnocks showed a positive linear
association with shrub cover, whereas both Lesser Whitethroat and Wren showed a
quadratic association, where the probability of occurrence of Lesser Whitethroat and Wren
peaked at c. 45% and c. 50% shrub cover respectively. The number of mature trees showed
a positive relationship with Chaffinch presence. There was also a negative effect of rock
cover on Tree Pipit occurrence. Altitude was the only variable within the full model which
was not linked to vegetation cover, and had different effects on the occurrence probability of
Chaffinch, Wren (negative) and Northern Wheatear and Water Pipit (positive).

Finescale habitat structure

Details of model-averaged parameters of the model set for finescale habitat structure are
given in the ESM Table S3. A number of dependent variables showed significant quadratic
effects (e.g. probability of occurrence or diversity peaking at intermediate frequencies), either
for all shrubs (Northern Wheatear), or for individual shrub species (Wren and Juniper
frequency, Dunnock and Rhododendron frequency, species diversity and Bilberry
frequency). Shrub height heterogeneity was positively correlated with Wren and Tree Pipit
presence. A positive relationship of canopy presence was found for bird species richness

and diversity, as well as for Chaffinch presence. In contrast, it showed a negative association with Northern Wheatear presence. Structural vegetation diversity was not selected in any model set (see ESM Table S3).

Combination of broadscale and finescale habitat structure

Details of significant model-averaged parameters of the final combined model sets are given in Table 2 (for a full list of parameters see ESM Table S4). In line with our expectation on effects of habitat mosaics on ecotone species, we here focus on shrub cover, but graphs of all significant variables in combined models are presented in ESM, Fig. S1. Shrub cover, as a broadscale variable, occurred in the combined model set for bird species diversity (Fig. 1) and Lesser Whitethroat (ESM Fig. S1). In a number of cases, individual bird species occurrences were closely associated either with shrub species identity or with shrub frequency (Table 2). Quadratic relationships between shrub species and bird species occurrence were found for Dunnock (Rhododendron), Wren (Juniper) and bird species diversity (Bilberry, see Fig. 2). Tree Pipit occurrence declined with increasing Rhododendron frequency (Fig. 2). Shrub height heterogeneity was closely related to Tree Pipit and Wren occurrences.

The frequency of canopy or the number of mature trees was retained in the combined models for bird species diversity, bird species richness and Chaffinch occurrence (positive associations) as well as for Dunnock occurrence (negative association). Altitude showed a negative relationship with the occurrence of Wren and Chaffinch, while it was positively associated with Northern Wheatear presence.

Model comparison

A summary of the ten highest ranked models for each species and each diversity measure across scales is shown in Fig. 3. The higher ranked models were mostly based on combined models (i.e. combinations of broad- and finescale variables), or broadscale models alone.

The best models ($\Delta AICc < 2$) for Dunnock, Lesser Whitethroat, Northern Wheatear, Tree Pipit, Chaffinch, Wren and species diversity contained only combined models. Finescale models were in the best model set only for species richness, but combined and broadscale models performed equally well (i.e. $\Delta AICc < 2$). Figure 3 also illustrates that, for many species, there was a high degree of model uncertainty in that there were often several models where $\Delta AICc < 2$. In general, finescale habitat variables of high weight that were present in the combined (best) models were related to the presence of shrubs either overall (Northern Wheatear) or of specific shrub species (Dunnock, Lesser Whitethroat, Tree Pipit, Wren and bird species richness and diversity; Table 3).

Discussion

The aim of this study was to describe species-specific habitat requirements within a mountainous forest-shrub ecotone in order to assess the relationships between the diversity and distributions of birds and environmental variables measured at different scales, and hence to identify potential conservation priorities and to inform future modelling methods. Through the combination of broad- and finescale habitat data in final models, we determined key habitat characteristics which shaped bird species richness and diversity. Furthermore, it enabled us to pinpoint habitat elements which are specifically required by common ecotone species. Our expectations of positive associations between bird community measures (diversity and individual species occurrence) and habitat complexity were partially met in terms of shrub cover and to a lesser extent shrub height heterogeneity, but there was no evidence that the diversity of vegetation structure was important.

Comparison of model scales

For making management recommendations, the identification of key habitat characteristics (e.g. vegetation structure or plant species composition) supporting bird species diversity or

target species is essential. The decision at which scale this objective will be addressed varies among studies representing a trade-off between broadscale (remote sensing techniques, Braunisch et al. 2016) and finescale data collection (detailed vegetation measurements in the field, Patthey et al. 2012). Both techniques show advantages and disadvantages. Collecting broadscale data (for example, through remote-sensed data bases) allows large areas to be covered, but has the potential to miss relevant habitat features. Data collection in the field provides more detailed information, but is time consuming and only applicable for smaller areas. Therefore choosing the appropriate scale is crucial as it directly determines the outcome of the study. The model scale comparison (broadscale, finescale or combined) applied on the same data allowed the assessment of the scale of data collection needed to identify habitat parameters determining bird species diversity or species specific habitat requirements in the forest-shrub ecotone.

The comparison revealed that combined and/or broadscale models always performed better than finescale models for individual species. When combined models performed best, variables linked to shrub species identity (finescale variables) were included in several cases (Dunnock, Lesser Whitethroat, Tree Pipit, Wren and bird species richness and diversity). Other finescale variables were rarely included in the combined model set for individual bird species, or alternatively could be substituted by equivalent broadscale variables which had been excluded from the modelling process because of high collinearity between variables (e.g Canfreq, a finescale variable which was highly correlated with canopy cover measured at the broadscale). Furthermore, finescale models were only included in the best model set (i.e. $\Delta AICc < 2$) for species richness, but combined and broadscale models performed equally well. Variables that described vegetation structural heterogeneity or diversity were only rarely included in the best model sets: SDshrubs was in the best model set for Wren, Tree Pipit and species diversity, although for the latter, the variable was not significant and was of low variable weight (ESM Tables S4 and S5).

These results therefore suggest that structural vegetation may be less important for the identification of factors determining species diversity and species distribution in the

majority of cases. However, to further our understanding of individual species and bird species diversity, data collection in the field should focus on habitat data which considers horizontal vegetation cover collected at a broad scale, but which includes species-specific estimates of cover of relevant shrub species in the area in order to model distributions of birds in the shrub-forest ecotone. The assessment of horizontal habitat cover can be done quickly and easily by eye from a single location for the whole area of a point count, including cover of easily recognizable shrub species such as Juniper and Rhododendron, whereas detailed structural vegetation measurements (as undertaken here) require considerable effort and access to a much greater area of a given point. The results further suggest that land cover datasets analogous to the data collected here should also be adequate for species distribution modelling in the studied habitat if they are able to estimate the cover of the dominant shrub species. Thus, broadscale habitat data and data on shrub species composition should provide a sufficient basis in identifying relevant species-specific habitat parameters in a mountain environment. Future species distribution models should seek to incorporate species-specific estimates of shrub cover, especially as the dominant species in the area are likely to respond differently to future climate change (Theurillat and Guisan 2001; Neuner 2014).

Factors affecting bird diversity and distribution at different habitat scales

There was some support that a habitat mosaic was beneficial for some individual species in that Dunnock, Lesser Whitethroat and Wren showed significant non-linear associations with either shrub cover or shrub species frequency in at least one model. Furthermore, shrub cover and frequency occurred in two final models and were positively correlated with bird species diversity (shrub cover) as well as Northern Wheatear presence (shrub frequency). The general overall importance of shrubs can easily be understood as they provide nesting habitat for shrub-nesting species, provide shelter in harsh weather conditions and can shield birds from predators.

In addition to overall shrub cover, individual shrub species were also important for some bird species. Bilberry cover was negatively related to bird species diversity, presumably because, in contrast to the other shrub species present, this species does not provide dense cover that could be suitable for nesting. Only Wren was positively associated with Juniper frequency. It was also negatively associated with altitude, which may suggest a link to the different growth characteristics of Juniper along the altitudinal gradient (Hallinger et al. 2010). At high altitudes (>2000m), this shrub species typically grows fairly low to the ground (10-30 cm; Aeschimann et al. 2004), which may make it unsuitable for nesting (due to predation risk for example). Suitable Wren nesting habitat may only be found at lower altitudes (1800 – 2000 m), where Juniper tends to be taller, and possibly less dense.

In contrast to Juniper, Rhododendron can still grow up to heights suitable for nesting (30 – 120 cm; Aeschimann et al. 2004) in the upper fringe of the ecotone and could therefore be seen as an attractive alternative for shrub-nesting species. In the combined models, Rhododendron showed a non-linear association with Dunnock presence, which seems to be preferred as a nesting habitat over other shrub species (pers. obs.). In the Alps, Rhododendron can form very large and dense patches on north, west and northwest-facing slopes within the subalpine belt (Pornon and Bernard 1996). Its distribution depends highly on winter snow cover which serves as a protective layer against excessive irradiation and frost (Neuner et al. 1999). However, due to climate change, snow cover is predicted to decrease by the end of the century (Beniston et al. 2003). Taking potential snow accumulation into account, Komac et al. (2016) showed that Rhododendron could experience an important reduction in its realized niche, and that its future habitat could be confined to areas which are today scree and rocky hillside habitats. This outcome suggests that, even if current habitat is maintained, climatic conditions might become less favourable for the persistence of Rhododendron and that suitable habitat for shrub-nesting species in the forest-shrub ecotone will disappear.

Conservation implications

451 The loss of open habitats due to abandonment of grazing (Gehrig-Fasel et al. 2007; Roura-
452 Pascual et al. 2004; MacDonald et al. 2000) and climate change (Lenoir et al. 2008; Pauli et
453 al. 2007) is likely to continue in the future to the extent that significant areas of more open
454 habitats, including the shrub-grassland ecotone, will be replaced by forest. To maintain
455 ecotone habitat, it may therefore be necessary to counteract shrub and indeed forest
456 encroachment in targeted areas in order to keep a heterogeneous character of the forest-
457 shrub ecotone. Possible methods to counteract shrub-encroached areas could be
458 mechanical shrub clearance or the re-establishment of grazing (e.g rotational grazing
459 systems with appropriate stocking level; Probo et al. 2014). However, mechanical shrub
460 clearance can only be applied if the required equipment can be transported to the
461 encroached areas, but accessibility by road is often limited in mountain areas. Moreover,
462 encroached areas are frequently characterized by a steep terrain, which influences the
463 effectiveness of traditional grazing practices, as livestock tends to concentrate in flat areas
464 and avoids steep slopes (Bailey et al. 1996, Mueggler 1965). Therefore, more specific
465 pastoral practices involving targeted grazing are needed. The strategic placement of mineral
466 mix supplements (MMS) would be one viable management option to be used in rugged
467 shrub-encroached locations (Pittarello et al. 2015). The placement of MMS would lead to
468 increased trampling in the surrounding 100 m of MMS site and therefore would reduce shrub
469 cover (Probo et al. 2013). A further more targeted option is the use of temporary night camp
470 areas (TNCA), where cows are fenced for up to two nights in shrub-encroached areas.
471 Through intense trampling within the fenced area, shrubs get mechanically damaged and
472 subsequently decrease in cover (Tocco et al. 2013; Pittarello et al. 2016, Probo et al. 2016).
473 In the long-term, this pastoral technique has the additional advantage that it increases plant
474 diversity (Pittarello et al. 2016), which in turn might positively influence invertebrate
475 availability (Tocco et al. 2013) for birds. Any such initiatives would have to be managed
476 carefully so as to open-up encroached areas whilst maintaining a reasonable level of shrub
477 cover. Similarly, grazing also has the potential to maintain open areas above the ecotone,
478 which is important for Northern Wheatear and Water Pipit which both are open habitat

species at high altitudes. Although, grazing could represent a viable management option in forest-ecotone areas, it is still unknown which potential direct or indirect effects it can have on different bird species groups (e.g. grassland, ecotone, forest) as it is likely that some species might be more affected than others. Moreover, grazing management targeted in the wrong areas, or applied at intensive levels, could also be detrimental to biodiversity.

It should be noted that habitat requirements among the most common bird species within the forest-shrub ecotone can differ considerably. Chamberlain et al. (2013) argued that management for the maintenance of high altitude grassland would be preferable to allowing forest expansion due to the high proportion of specialist species and species of conservation concern that could be negatively impacted. However, our data showed that forested areas with high shrub cover had the highest bird diversity. Nevertheless, the ecotone holds important bird species that were not well covered by our methods (von dem Bussche et al. 2008; Braunisch et al. 2016), and also has a high biodiversity of other taxa (Dirnböck et al. 2011). In order to meet a range of species-specific habitat requirements, it might therefore be important to sustain a high level of heterogeneity and to maintain a habitat mosaic within the ecotone (Patthey et al. 2012). Management recommendations need to be adopted for areas differing in altitude, topography, shrub species composition and the degree of shrub encroachment at appropriate scales (Braunisch et al. 2016). Depending on the targeted area, it might therefore be necessary to apply a combination of different management techniques and to adjust the time period of application to promote heterogeneity. There is the possibility of managing for diverse landscapes that can incorporate a range of needs for different habitat types which facilitates species resilience and resistance to environmental change (e.g. Brambilla et al. 2017), but further work is needed on the most appropriate scale of management by which this can be achieved.

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Table 1 Variables considered in the analysis, and the scale at which they were measured. The broadscale category was measured at the whole point count location scale and finescale category was measured at the plot level (n = 11 for each point)

Parameter	Category	Description
Canopy	Broadscale	Percentage cover of canopy (above head height) within a radius of 100 m of the point count centre
Shrubs	Broadscale	Percentage cover of shrubs within a radius of 100 m of the point count centre
Trees	Broadscale	Number of mature (greater than c. 20 cm in diameter) trees within a radius of 50 m of the point count centre
Rocks	Broadscale	Percentage cover of rocks within a radius of 100 m of the point count centre
HCOV	Broadscale	Shannon Index of broadscale habitat diversity ($H' = - \sum p_i \ln p_i$, where p_i is the percentage cover of the different habitat types)
Alt	Broadscale	Altitude of the point count location in meters asl. estimated from a GPS
H1	Finescale	Shannon Index of vegetation density diversity at 1 m above the ground
H05	Finescale	Shannon Index of vegetation density diversity at 0,5 m
SDShrub	Finescale	Shrub height heterogeneity measured as the standard deviation of the average shrub height at the point count location
Canfreq	Finescale	Frequency of vegetation sampling points for a point count location where canopy was present
Shrubfreq	Finescale	Frequency of vegetation sampling points for a point count location where shrubs were present
Rodfreq	Finescale	Proportion of vegetation sampling points for a point count location where Rhododendron was the dominant shrub species
Junfreq	Finescale	Frequency of vegetation sampling points for a point count location where Juniper was the dominant shrub species
Bilfreq	Finescale	Frequency of vegetation sampling points for a point count location where bilberry was the dominant shrub species

Table 2 Final significant model-averaged parameters of the model set derived by combining significant model-averaged parameters of broadscale and finescale habitat structure model sets for bird diversity, richness and the commonest species in the study area. The scale (B = broadscale, F= finescale), estimate, standard error (SE), test value (z) and p value are given for each parameter. Full details for all species and parameters are given in Table S4

Dependent Variable	Parameter	Scale	Estimate \pm SE	z	p
Lesser Whitethroat	Shrubs	B	2.171 \pm 0.729	2.930	0.003
	Shrubs ²	B	-2.041 \pm 0.823	2.439	0.015
Tree Pipit	Rock	B	-1.416 \pm 0.648	2.151	0.032
	SDshrub	F	1.438 \pm 0.514	2.754	0.006
	Rodfreq	F	-1.120 \pm 0.480	2.296	0.022
Dunnock	Trees	B	-0.939 \pm 0.471	1.963	0.050
	Rodfreq	F	1.601 \pm 0.672	2.351	0.019
	Rodfreq ²	F	-1.363 \pm 0.589	2.286	0.022
Northern Wheatear	Alt	B	2.872 \pm 0.482	5.873	\leq 0.000
	Shrubfreq	F	-2.325 \pm 0.469	4.884	\leq 0.000
	Shrubfreq ²	F	-0.618 \pm 0.031	19.595	\leq 0.000
Wren	Alt	B	-2.435 \pm 0.875	2.747	0.006
	Junfreq ²	F	0.583 \pm 0.291	1.974	0.048
	SDshrub	F	1.096 \pm 0.549	1.969	0.049
Chaffinch	Alt	B	-1.533 \pm 0.409	3.687	\leq 0.000
	Canfreq	F	1.238 \pm 0.404	3.016	0.003
Species richness	Canfreq	F	0.169 \pm 0.059	2.838	0.005
Species diversity	Shrubs	B	0.221 \pm 0.062	3.508	\leq 0.000
	Canfreq	F	0.131 \pm 0.053	2.451	0.014
	Bilfreq	F	-0.171 \pm 0.056	2.990	0.003
	Bilfreq ²	F	-0.063 \pm 0.025	2.491	0.013

Table 3 Variables with the highest importance (Akaike weight > 0.70) for combined models, derived from all combinations of models for each dependent variable, grouped according to whether they were broad- or finescale. Full details are given in ESM Table S5. A dash indicates Akaike weight < 0.70 for a given scale. Variable codes are given in Table 1 and Table S1

Variable	Broadscale	Finescale
Tree Pipit	Rock, Shrubs ²	SDShrub, Rodfreq
Water Pipit	Alt	Canfreq
Dunnock	Trees	Rodfreq, Rodfreq ²
Northern Wheatear	Alt	Shrubfreq
Lesser Whitethroat	Shrubs, Shrubs ²	-
Wren	Alt, Shrubs	SDShrub, Junfreq ²
Chaffinch	Alt	Canfreq
Species richness	-	Canfreq
Species diversity	Shrubs	-

Figure legends

Fig. 1

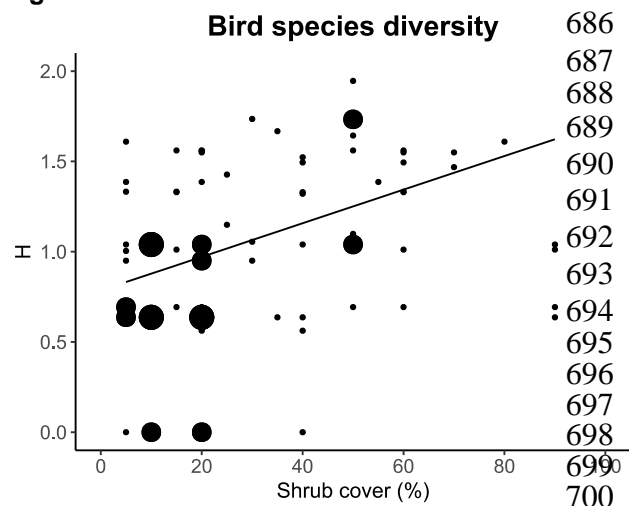
Relationship between shrub cover (%) and bird species diversity based on the combined model. Black circles represent the H-value in relation to shrub cover for a given point count, where the size of the circle is proportional to the number of points for a given H-value at a particular level of shrub cover

Fig. 2

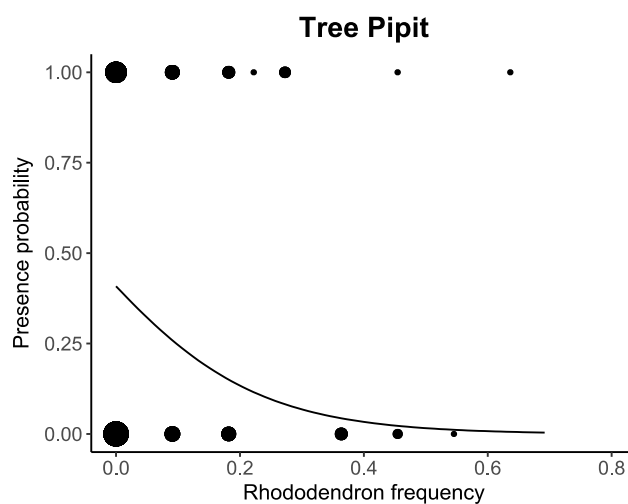
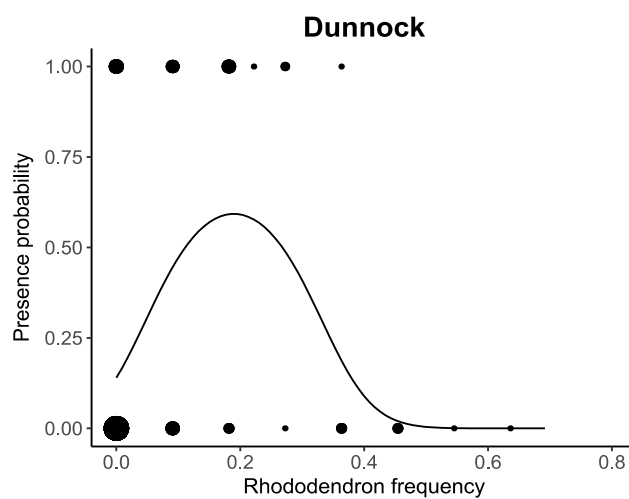
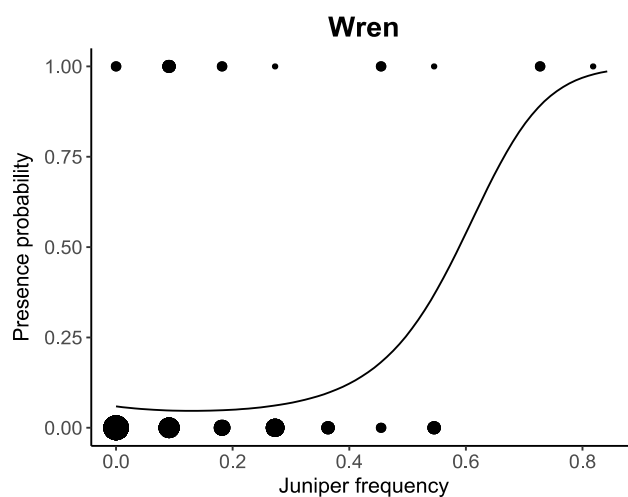
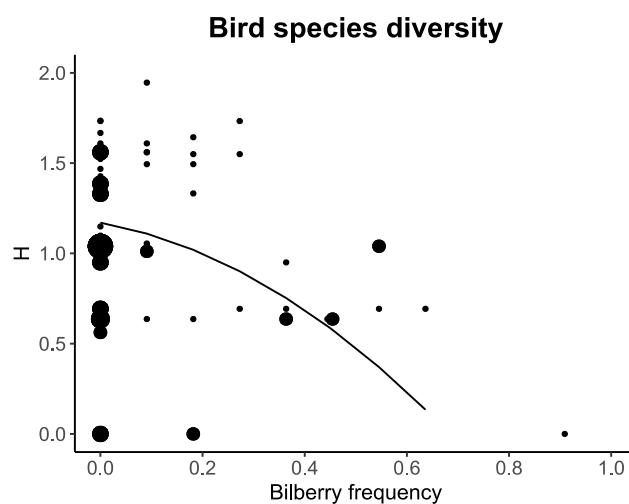
Relationship between shrub species frequency (Rhododendron, Juniper, bilberry) and the probability of occurrence for individual bird species (Dunnock, Tree Pipit, Wren) and bird species diversity based on combined models. Black circles represent the point counts where a species was present/absent in relation to shrub species frequency, and the size of the circle is proportional to the number of points for a given category of presence/absence at a particular level of shrub frequency. For bird species diversity, black circles represent the H-value in relation to bilberry frequency, where the size of the circle is again proportional to the number of points for a given H-value at a particular level of bilberry frequency.

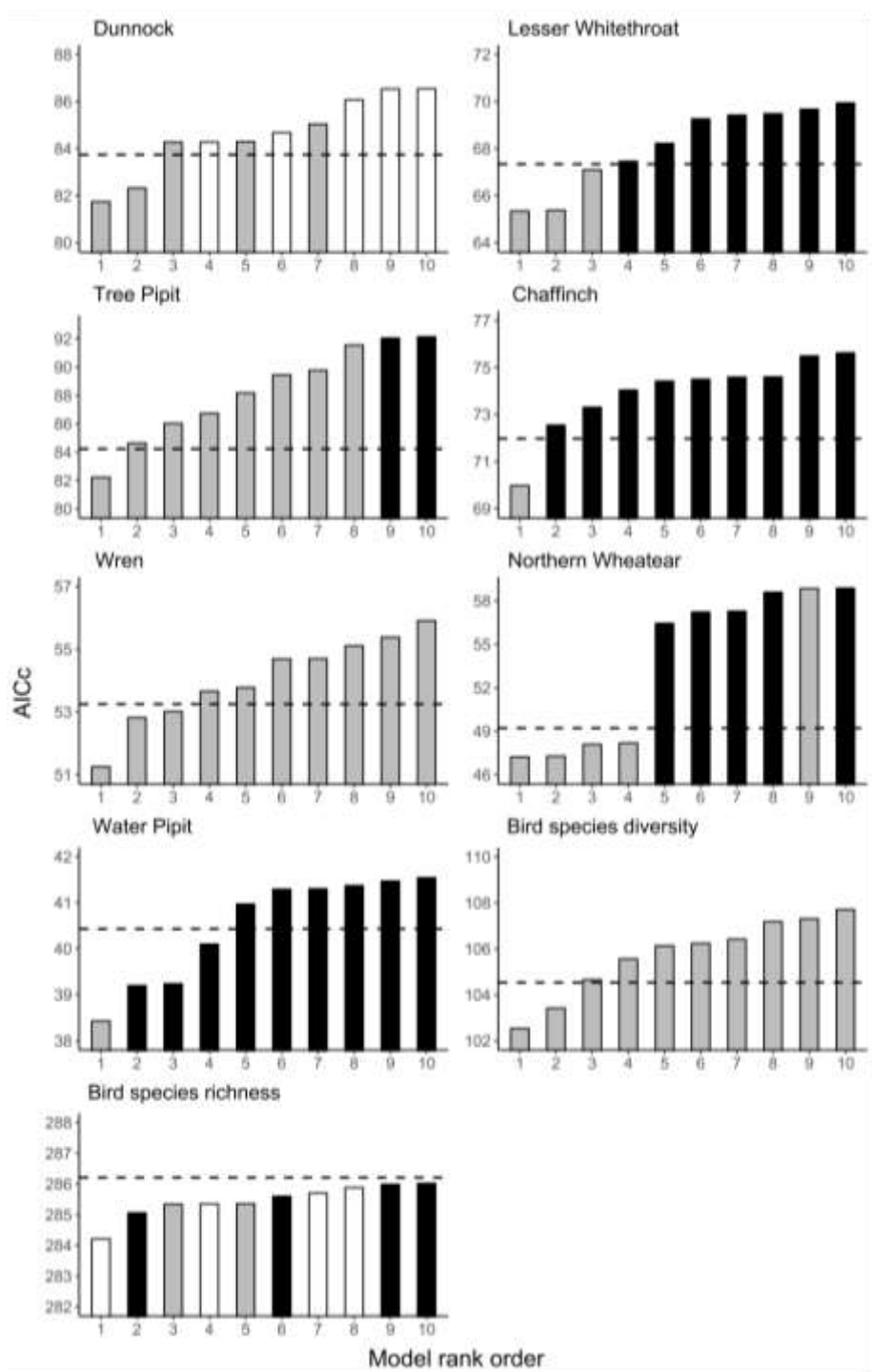
Fig. 3 The ten best ranked models according to AICc (where smaller AICc values indicate better performing models) for individual species, and for species richness and diversity. Each model is classified according to whether variables were finescale (white bars), broadscale (black bars) or a combination of the two (grey bars) in each model. The dashed horizontal line indicates $\Delta AICc = 2$ (i.e. models below the line are considered to be in the best model set)

685 **Fig. 1**



705 **Fig. 2**





Electronic Supplementary Material – Journal of Ornithology

The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone

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Table S1 Variables which were removed after VIF and correlation coefficient calculations, or during the model reduction process. The broadscale category was measured at the whole point count location scale and finescale category was measured at the plot level (n = 11 for each point)

Parameter	Category	Description
Grass	Broadscale	Percentage cover of grass within a radius of 100 m of the point count centre
H0	Finescale	Shannon-Index of vegetation density diversity at ground level
Altgrs	Finescale	Average grass height across the plots at each point count location
Altshrub	Finescale	Average shrub height across the plots at each point count location
SDgrs	Finescale	Standard deviation of the average grass height at the point count location
Othfreq	Finescale	Frequency of vegetation sampling points for a point count location where shrubs different from Juniper, Rhododendron and bilberry were the dominant shrub species

Table S2 Model-averaged estimates of the model set for broadscale habitat structure presented for bird diversity, richness and the commonest species in the study area. The estimate, standard error (SE), test value (z) and p value are given for each parameter

Dependent Variable	Parameter	Estimate \pm SE	z	p
Tree Pipit	Alt	-0.559 \pm 0.355	1.552	0.121
	Trees	0.247 \pm 0.308	0.790	0.429
	Shrubs	0.292 \pm 0.497	0.583	0.560
	Shrubs ²	0.905 \pm 0.480	1.857	0.063
	Rock	-1.403 \pm 0.616	2.243	0.025
	HCOV	0.445 \pm 0.420	1.047	0.295
Water Pipit	Alt	2.095 \pm 1.014	2.036	0.042
	Trees	-18.384 \pm 16.692	1.085	0.278
	Shrubs	-0.851 \pm 0.777	1.081	0.280
	Shrubs ²	-0.418 \pm 0.849	0.485	0.627
	Rock	0.185 \pm 0.769	0.238	0.812
	HCOV	-0.714 \pm 0.661	1.065	0.287
Dunnock	Alt	0.547 \pm 0.468	1.154	0.249
	Trees	-1.136 \pm 0.511	2.191	0.028
	Shrubs	1.029 \pm 0.466	2.183	0.029
	Shrubs ²	-0.335 \pm 0.387	0.857	0.391
	Rock	-0.693 \pm 0.527	1.298	0.194
	HCOV	0.585 \pm 0.423	1.365	0.172
Northern Wheatear	Alt	1.907 \pm 0.789	2.384	0.017
	Trees	-2.382 \pm 1.658	1.418	0.156
	Shrubs	-1.661 \pm 1.020	1.613	0.107
	Shrubs ²	-0.453 \pm 0.988	0.452	0.651
	Rock	-0.774 \pm 0.768	0.997	0.319
	HCOV	1.071 \pm 0.908	1.168	0.243
Lesser Whitethroat	Alt	0.331 \pm 0.496	0.658	0.511
	Trees	-0.257 \pm 0.397	0.639	0.523
	Shrubs	1.914 \pm 0.757	2.492	0.013
	Shrubs ²	-1.758 \pm 0.834	2.075	0.038
	Rock	0.048 \pm 0.480	0.098	0.922
	HCOV	0.731 \pm 0.550	1.313	0.189
Wren	Alt	-2.263 \pm 0.663	3.358	0.001
	Trees	0.015 \pm 0.385	0.039	0.969
	Shrubs	2.204 \pm 0.897	2.421	0.015
	Shrubs ²	-1.351 \pm 0.630	2.109	0.035

Chaffinch	Rock	-0.080 ± 0.784	0.100	0.920
	HCOV	0.208 ± 0.649	0.317	0.751
	Alt	-1.638 ± 0.509	3.177	0.001
	Trees	1.141 ± 0.497	2.261	0.024
	Shrubs	0.458 ± 0.399	1.129	0.259
	Shrubs ²	0.181 ± 0.338	0.530	0.596
Rock Bunting	Rock	-0.234 ± 0.474	0.486	0.627
	HCOV	0.561 ± 0.467	1.185	0.236
	Alt	-0.388 ± 0.419	0.912	0.362
	Trees	0.380 ± 0.353	1.062	0.288
	Shrubs	0.672 ± 0.492	1.348	0.178
	Shrubs ²	-0.152 ± 0.378	0.398	0.690
Species diversity	Rock	0.746 ± 0.376	1.955	0.051
	HCOV	0.376 ± 0.376	0.987	0.324
	Alt	-0.125 ± 0.053	2.320	0.020
	Trees	0.139 ± 0.054	2.524	0.012
	Shrubs	0.221 ± 0.081	2.706	0.007
	Shrubs ²	-0.116 ± 0.049	2.317	0.021
Species richness	Rock	-0.044 ± 0.060	0.721	0.471
	HCOV	0.084 ± 0.063	1.319	0.187
	Alt	-0.097 ± 0.082	1.170	0.242
	Trees	0.134 ± 0.064	2.066	0.039
	Shrubs	0.180 ± 0.095	1.876	0.061
	Shrubs ²	-0.103 ± 0.075	1.359	0.174
	Rock	-0.023 ± 0.079	0.282	0.778
	HCOV	0.057 ± 0.090	0.621	0.535

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Table S3 Model-averaged parameters of the model set for finescale habitat structure presented for bird diversity, richness and the commonest species in the study area. The estimate, standard error (SE), test value (z/t) and p value are given for each parameter

Dependent Variable	Parameter	Estimate \pm SE	z / t	p
Lesser Whitethroat	SDshrub	0.144 \pm 0.296	0.477	0.633
	Bilfreq	-0.375 \pm 0.681	0.543	0.587
	Bilfreq ²	-1.364 \pm 1.199	1.119	0.263
	H05	0.251 \pm 0.256	0.966	0.334
	H1	0.290 \pm 0.272	1.047	0.295
	Canfreq	0.069 \pm 0.318	0.214	0.831
Tree Pipit	SDshrub	1.564 \pm 0.534	2.889	0.004
	Rodfreq	-1.007 \pm 0.544	1.827	0.068
	Rodfreq ²	0.167 \pm 0.278	0.593	0.553
	H05	0.481 \pm 0.387	1.223	0.221
	H1	0.415 \pm 0.344	1.187	0.235
	Canfreq	0.090 \pm 0.315	0.280	0.779
Dunnock	SDshrub	-0.614 \pm 0.497	1.215	0.224
	Rodfreq	2.036 \pm 0.670	2.995	0.003
	Rodfreq ²	-1.665 \pm 0.551	2.974	0.003
	H05	0.086 \pm 0.309	0.275	0.783
	H1	0.002 \pm 0.377	0.006	0.995
	Canfreq	-0.181 \pm 0.356	0.501	0.617
Rock Bunting	SDshrub	-0.220 \pm 0.447	0.486	0.627
	Shrubfreq	-0.270 \pm 0.357	0.746	0.456
	Shrubfreq ²	-0.300 \pm 0.357	0.827	0.408
	H05	-0.063 \pm 0.335	0.184	0.854
	H1	-0.168 \pm 0.364	0.453	0.650
	Canfreq	0.442 \pm 0.328	1.328	0.184
Northern Wheatear	SDshrub	-0.925 \pm 0.727	1.253	0.210
	Shrubfreq	-0.646 \pm 0.570	1.115	0.265
	Shrubfreq ²	-1.077 \pm 0.491	2.157	0.031
	H05	0.254 \pm 0.403	0.620	0.535
	H1	0.075 \pm 0.669	0.110	0.912
	Canfreq	-2.454 \pm 0.932	2.592	0.010
Wren	SDshrub	0.970 \pm 0.416	2.329	0.020
	Junfreq	0.113 \pm 0.565	0.198	0.843
	Junfreq ²	0.502 \pm 0.236	2.128	0.033
	H05	-0.012 \pm 0.351	0.032	0.974

Chaffinch	H1	0.252 ± 0.312	0.795	0.427
	Canfreq	0.205 ± 0.401	0.505	0.614
	SDshrub	-0.027 ± 0.389	0.070	0.945
	Shrubfreq	-0.462 ± 0.328	1.389	0.165
	Shrubfreq ²	0.328 ± 0.313	1.031	0.303
Water Pipit	H05	-0.337 ± 0.313	1.061	0.289
	H1	-0.279 ± 0.384	0.716	0.474
	Canfreq	1.738 ± 0.444	3.855	≤ 0.000
	SDshrub	0.340 ± 0.676	0.582	0.561
	Bilfreq	0.600 ± 0.466	1.270	0.204
Species diversity	Bilfreq ²	0.020 ± 0.250	0.079	0.937
	H05	1.105 ± 3288.174	0.000	1.000
	H1	11.995 ± 2901.247	0.004	0.997
	Canfreq	-51.512 ± 8599.602	0.006	0.995
	SDshrub	0.110 ± 0.064	1.699	0.089
Species richness	Bilfreq	-0.100 ± 0.065	1.526	0.127
	Bilfreq ²	-0.054 ± 0.023	2.350	0.019
	H05	-0.094 ± 0.052	1.769	0.078
	H1	0.040 ± 0.062	0.642	0.521
	Canfreq	0.178 ± 0.053	3.293	0.001
	SDshrub	0.068 ± 0.071	0.945	0.345
	Bilfreq	-0.057 ± 0.116	0.483	0.629
	Bilfreq ²	-0.073 ± 0.050	1.444	0.149
	H05	-0.065 ± 0.069	0.936	0.349
	H1	0.024 ± 0.068	0.358	0.721
	Canfreq	0.153 ± 0.064	2.349	0.019

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Table S4 Final model-averaged parameters of the model set derived by combining significant model-averaged parameters of broadscale and finescale habitat structure, and top model sets for bird diversity, richness and the commonest species in the study area. The scale (B = broadscale, F= finescale), estimate, standard error (SE), test value (z) and p value are given for each parameter

Dependent Variable	Parameter	Scale	Estimate \pm SE	z	p
Lesser Whitethroat	Shrubs	B	2.171 \pm 0.729	2.930	0.003
	Shrubs ²	B	-2.041 \pm 0.823	2.439	0.015
	Bilfreq	F	-0.893 \pm 0.685	1.284	0.199
	Bilfreq ²	F	-0.926 \pm 0.960	0.949	0.343
Tree Pipit	Rock	B	-1.416 \pm 0.648	2.151	0.032
	SDshrub	F	1.438 \pm 0.514	2.754	0.006
	Shrubs	B	0.222 \pm 0.457	0.478	0.632
	Shrubs ²	B	0.748 \pm 0.427	1.721	0.085
Dunnock	Rodfreq	F	-1.120 \pm 0.480	2.296	0.022
	Trees	B	-0.939 \pm 0.471	1.963	0.050
	Shrubs	B	0.808 \pm 0.485	1.646	0.010
	Rodfreq	F	1.601 \pm 0.672	2.351	0.019
Northern Wheatear	Rodfreq ²	F	-1.363 \pm 0.589	2.286	0.022
	Alt	B	2.872 \pm 0.482	5.873	\leq 0.000
	Shrubfreq	F	-2.325 \pm 0.469	4.884	\leq 0.000
	Shrubfreq ²	F	-0.618 \pm 0.031	19.595	\leq 0.000
Wren	Canfreq	F	-1.239 \pm 0.700	1.742	0.082
	Alt	B	-2.435 \pm 0.875	2.747	0.006
	SDshrub	F	1.096 \pm 0.549	1.969	0.049
	Shrubs	B	1.649 \pm 0.923	1.765	0.078
	Shrubs ²	B	-1.095 \pm 0.712	1.516	0.129
	Junfreq	F	0.306 \pm 0.761	0.399	0.690
Chaffinch	Junfreq ²	F	0.583 \pm 0.291	1.974	0.048
	Alt	B	-1.533 \pm 0.409	3.687	\leq 0.000
	Canfreq	F	1.238 \pm 0.404	3.016	0.003
Water Pipit	Alt	B	1.926 \pm 0.985	1.925	0.054
	Canfreq	F	-48.267 \pm 14751.960	0.003	0.997
Species richness	Shrubs	B	0.095 \pm 0.063	1.481	0.139
	Canfreq	F	0.169 \pm 0.059	2.838	0.005
Species diversity	Alt	B	-0.065 \pm 0.062	1.039	0.299

SDshrub	F	0.066 ± 0.060	1.090	0.276
H05	F	-0.081 ± 0.048	1.657	0.097
Shrubs	B	0.221 ± 0.062	3.508	≤ 0.000
Shrubs ²	B	-0.083 ± 0.047	1.739	0.082
Canfreq	F	0.131 ± 0.053	2.451	0.014
Bilfreq	F	-0.171 ± 0.056	2.990	0.003
Bilfreq ²	F	-0.063 ± 0.025	2.491	0.013

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Table S5 Variables weights across all combinations of models, considering either broadscale, finescale or combined models. Weights were calculated based on Akaike weights for each model, which is expressed as the likelihood contribution of each model as a proportion of the summed likelihood contributions of all models. The weight for each variable is the sum of model weights for all models in which a given variable was present (Burnham & Anderson 2002). Output is shown only if a given model type was amongst the top model set (i.e. $\Delta AICc < 2$). For example, no broadscale or finescale models were in the best model set for Dunnock (see Fig. 3), hence variable weights are presented only for combined models. A missing value indicates that a variable was not included in the model averaging procedure for that particular species/scale. Variables are defined in Table 1 and Table S3

(a) Broadscale

Variable	Alt	HCOV	Rock	Shrubs	Shrubs ²	Trees
Water Pipit	0.92	0.40	0.28	0.45	0.29	0.90
Species richness	0.42	0.33	0.26	0.78	0.52	0.71

(b) Finescale

Variable	Canfreq	H05	H1	Bilfreq	Bilfreq ²	SDshrub
Species richness	0.82	0.34	0.26	0.35	0.57	0.35

Broadscale						Finescale										
Variable	Alt	Rock	Shrubs	Shrubs ²	Trees	Shrubfreq	Shrubfreq ²	H05	Canfreq	Junfreq	Junfreq ²	Rodfreq	Rodfreq ²	SDshrub	Bilfreq	Bilfreq ²
Tree Pipit	-	0.97	0.26	0.84	-	-	-	-	-	-	-	0.94	-	0.99	-	-
Lesser Whitethroat	-	-	1.00	1.00	-	-	-	-	-	-	-	-	-	-	0.51	0.52
Dunnock	-	-	0.60	-	0.80	-	-	-	-	-	-	0.86	0.97	-	-	-
Northern Wheatear	1.00	-	-	-	-	1.0	0.39	-	0.50	-	-	-	-	-	-	-
Wren	1.00	-	0.74	0.63	-	-	-	-	-	0.34	0.82	-	-	0.88	-	-
Water Pipit	0.98	-	-	-	-	-	-	-	0.97	-	-	-	-	-	-	-
Chaffinch	1.00	-	-	-	-	-	-	-	0.99	-	-	-	-	-	-	-
Species diversity	0.07	-	0.95	0.13	-	-	-	0.13	0.48	-	-	-	-	0.08	0.67	0.25
Species richness	-	-	0.51	-	-	-	-	-	0.95	-	-	-	-	-	-	-

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Table S6 Observed and expected values of Moran's I and associated P-values to test for spatial autocorrelation. Tests were based on residuals from the full model for each scale and each species

Species	Broadscale			Finescale			Combined		
	obs	exp	p	obs	exp	p	obs	exp	p
Lesser Whitethroat	0.014	-0.013	0.073	0.028	-0.013	0.007	0.022	-0.013	0.022
Tree Pipit	0.012	-0.013	0.954	-0.019	-0.013	0.707	-0.015	-0.013	0.886
Dunnock	0.002	-0.013	0.345	0.001	-0.013	0.356	0.004	-0.013	0.272
Chaffinch	0.003	-0.013	0.529	0.008	-0.013	0.166	0.014	-0.013	0.076
Wren	0.003	-0.013	0.518	-0.019	-0.013	0.680	-0.013	-0.013	0.988
Northern Wheatear	0.002	-0.013	0.455	-0.021	-0.013	0.578	-0.020	-0.013	0.619
Water Pipit	0.008	-0.013	0.721	-0.017	-0.013	0.802	0.006	-0.013	0.210
Species diversity	0.020	-0.013	0.646	-0.022	-0.013	0.542	-0.027	-0.013	0.347
Species richness	0.023	-0.013	0.503	-0.016	-0.013	0.849	-0.020	-0.013	0.628

There was only a single significant result, for the finescale model for Lesser Whitethroat. In this case, models were re-run accounting for spatial effects by adding a smoothed interactive effect of latitude and longitude in a Generalized Additive Mixed Model using the gamm command in the package gamm4 (Wood & Scheipl 2017). This made no difference to the model outcome in terms of significance levels (Table S6), and parameter estimates were similar. We therefore conclude that for this species, the significant spatial autocorrelation detected did not have an effect on model outcomes.

Table S7 A comparison of models predicting Lesser Whitethroat occurrence in relation to finescale habitat variables without (standard model) and with (spatial model) accounting for spatial effects. For variable definitions, see Table 1

Variable	Standard model				Spatial model			
	Parameter	SE	z	P	Parameter	SE	z	P
Intercept	-0.711	0.601	-1.183	0.237	-0.887	0.678	-1.130	0.195
H05	0.205	0.274	0.749	0.454	0.058	0.305	0.191	0.849
H1	0.273	0.316	0.874	0.382	0.516	0.368	1.399	0.166
Bilfreq	0.143	0.757	0.189	0.850	0.184	0.827	0.222	0.825
Bilfreq ²	-1.547	1.290	-1.119	0.230	-1.639	1.349	-1.215	0.229
SDshrub	0.025	0.334	0.074	0.941	0.093	0.358	0.259	0.797
Canfreq	-0.059	0.353	-0.168	0.867	-0.158	0.390	-0.450	0.687

Reference

Wood S, Scheipl F (2017) Generalized Additive Mixed Models using 'mgcv' and 'lme4'. R package version 0.2-2, URL <http://CRAN.R-project.org/package=gamm4>

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The contribution of broadscale and finescale habitat structure to the distribution and diversity of birds in an Alpine forest-shrub ecotone

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ESM Fig. S1

Relationship between significant model-averaged parameters of the combined model set for bird species richness, diversity and individual bird species. For individual bird species, black circles represent the point counts where a species was present/absent in relation to the relevant variable. The size of the circle is proportional to the number of points for a given category of presence/absence at a particular level of the respective variable. For bird species richness and diversity, black circles represent the H-value (diversity) or the number of bird species (richness) in relation to canopy frequency for a given point count, where the size of the circle is proportional to the number of points for a given H-value (diversity) or species number (richness) at a particular level of canopy frequency.

